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# Tritrophic niches of insect herbivores in an era of rapid environmental change

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A multi-trophic perspective improves understanding of the ecological and evolutionary consequences of rapid environmental change on insect herbivores. Loss of specialized enemies due to human impacts is predicted to dramatically reduce the number of tritrophic niches of herbivores compared to a bitrophic niche perspective. Habitat fragmentation and climate change promote the loss of both specialist enemies and herbivores, favoring ecological generalism across trophic levels. Species invasion can fundamentally alter trophic interactions toward various outcomes and contributes to ecological homogenization. Adaptive evolution on ecological timescales is expected to dampen tritrophic instabilities and diversify niches, yet its ability to compensate for tritrophic niche losses in the short term is unclear.

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## Introduction

The role of natural enemies in controlling herbivore populations fundamentally informs the structure and dynamics of ecological systems, underlying such basic observations as the relative 'greenness' of the (terrestrial) world [1] and providing the theoretical underpinning for biological control. Indeed, top-down effects of predators and parasitoids on insect herbivore fitness may be as important as bottom-up factors of plants and habitats [2]. Less broadly appreciated are the evolutionary consequences of top-down dimensions of the niches of herbivorous insects. From an evolutionary perspective, selection from enemies is an additional, complementary axis of niche differentiation upon which the process of adaptive radiation can drive diversification [3]. Importantly, direct and indirect interactions between enemies and plants create evolutionary opportunities for adaptation, divergence, and niche partitioning that underlie the enormous diversity of phytophagous insects [4••].

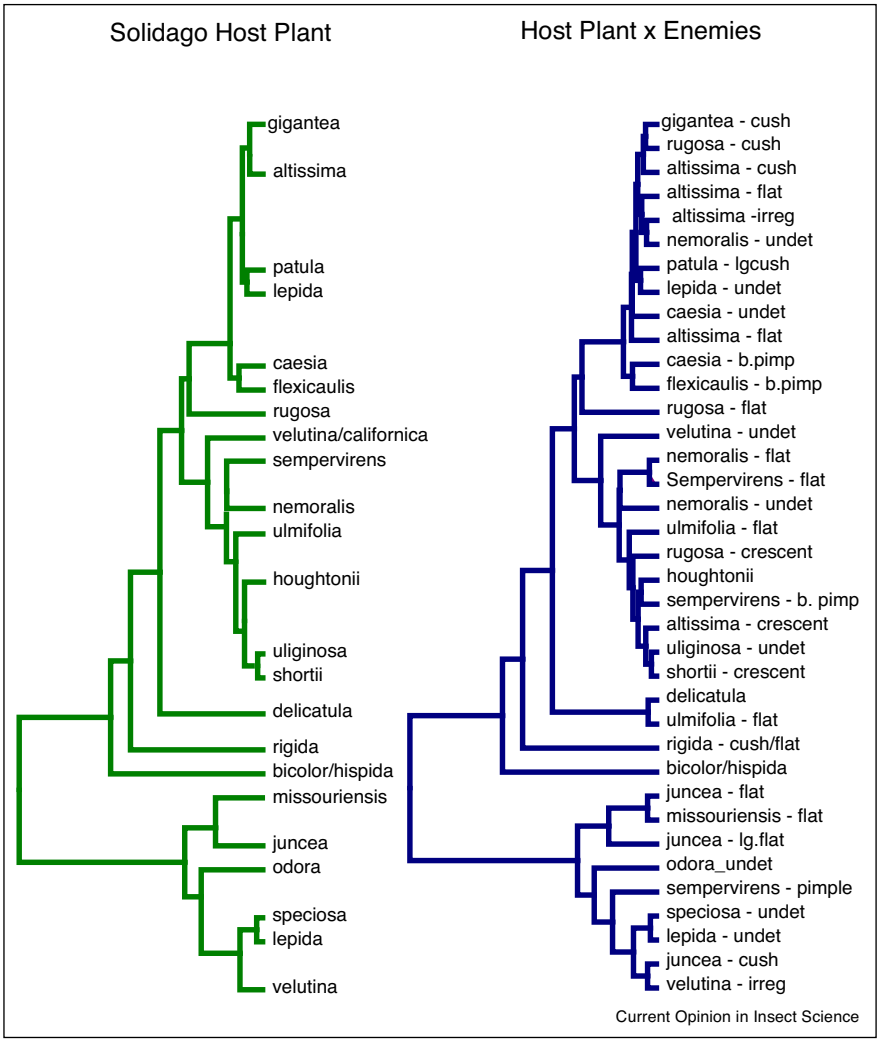
Ecological communities and their multitrophic networks are experiencing some of the most dramatic environmental changes in Earth's history. Anthropogenic environmental changes including habitat fragmentation and loss, climate change, and alien species invasion are fundamentally reshaping ecological communities and altering ecological interactions. Here we aim to review the tritrophic niche concept for phytophagous insects and its implications for understanding herbivore niches, evaluate how tritrophic communities and interactions are being affected by anthropogenic environmental impacts, and predict ecological and evolutionary consequences of these changes.

## The tritrophic niche

Inherent in the tritrophic niche concept is the view that ecological niches are neither a property of individual species nor of particular environments, but of ecological communities. Thus, their quantity and quality are determined critically by species interactions in addition to the abiotic environment. The value of a tritrophic perspective in understanding ecological niches of phytophagous insects has long been recognized if not stated explicitly [5,6]. Adoption of this view has led to the development of such influential concepts as enemy-free space (EFS; [7]), apparent competition [8], the slow-growth-high-mortality hypothesis (SGHM; [9]), and the 'tritrophic interactions hypothesis' [10]. Multitrophic perspectives can also illuminate adaptive evolutionary diversification of insect lineages [3,11] (Figure 1). As more studies explicitly consider both top-down and bottom-up factors, it is increasingly apparent that this broad perspective is necessary to understand the evolution and structure of herbivore communities.

Recent evidence for the tritrophic nature of herbivore niches comes from a variety of insect-plant systems. For example, niches of *Timema* walking sticks, a model for ecological speciation, are defined by their color patterns, host plants, and predation by birds [12]. Mismatches in these three components result not only in reduced *Timema* fitness, but also affect community diversity and processes [13]. Likewise, divergent host-plant specialization of pea aphid races is reinforced by escape from

**Figure 1**




An illustration of the multiplicative effects of host-plants and enemies in creating niches and driving adaptive diversification using *Asteromyia* gall midges on goldenrods (*Solidago* spp.). On the left is phylogenetic structure that can be attributed to differences host plant use (i.e. each lineage occupies a different host), on the right is phylogenetic structure attributable to the interaction between host-plants and enemies manifested by gall morphotypes (i.e. each lineage comprises a population defined by a particular host-plant and defensive gall morph combination). Gall morphotypes are indicated to the right, for example, cush = cushion, irreg = irregular, lg = large, pimp = pimple, undet = undefined. See Stireman *et al*. [11] for a more detailed examination of these patterns.

natural enemies [14•]. Perhaps most elegantly illustrating the tritrophic niche concept are *Blepharoneura* fruit flies that have radiated extensively into highly specific niches defined by host species, host plant part, and invulnerability to all but select specialized parasitoids [4••] (Box 1). Although most studies have shown that enemies favor narrower host-plant niches in herbivores, several studies also point to enemies as a factor promoting or maintaining broad diet breadths (e.g. [15,16,17•]).

While focused studies of community modules reveal much about the interplay between plants and enemies in molding herbivore niches, studies of broader communities are revealing how tritrophic interactions scale up. For example, studies of parasitism, predation and host-plant use across a community of forest caterpillars have shown that parasitism of dietary generalists varies across host tree species [18], lower predation risk by birds for specialized caterpillars is associated with host-plant-dependent defenses (e.g. crypsis; [19]), and diet breadth predicts susceptibility of caterpillars to different types of predators [20•]. Analysis of caterpillar communities has also demonstrated that apparent competition between herbivores through shared parasitoids can predict future abundance and parasitism rate [21•].

**Box 1 .**

Condon *et al.* [4••] show evidence for 14 herbivore niches (species of *Blepharoneura* flies) occupying two plant species (*Gurania* vines) and 4 plant phenotypes (male and female flowers of each of two species, *G. acuminata* and *G. spinulosa*). There is a single, unique host-specific parasitoid species (*Bellopius* wasps) that successfully parasitizes each herbivore species, and these highly specific parasitoid–herbivore interactions are responsible for ultrafine partitioning of tritrophic niches of the herbivores. We highlight these details to imagine how this intricately structured community module might be affected by rapid anthropogenic environmental change, which renders its most severe negative impacts on ecologically specialized species at higher trophic levels (see main text). If we imagine that the 14 host-specific parasitoids were immediately lost from the community due to human impacts, the number of herbivore niches (now bitrophic rather than tritrophic) would drop by an order of magnitude (to 2–4, the latter if the flies partition the plant by phenotype). This scenario inspires the graphical hypothesis in Figure 2, which compares the magnitude of predicted herbivore niche loss due to human impacts between bitrophic and tritrophic scenarios. Although the multiplicative effect of enemies on niche diversity implies that the loss of specific tritrophic interactions has the potential to greatly reduce the niche diversity of herbivores, the magnitude of this reduction is uncertain. The case in Condon *et al.* [4••] suggests that tritrophic niches can outnumber plant-based niches by a ratio of 3.5–7 to one. By contrast, the case illustrated in Figure 1 shows 37 herbivore populations (*Asteromyia* flies occupying tritrophic niches; 11) associated with 23 *Solidago* species (assumed to represent bitrophic niches), a ratio of 1.6 to one. These estimates suggest there may be ca. 1.5–7 tritrophic niches of herbivore per host-plant species per herbivore lineage (e.g. genus). However, in both cases is it unlikely that all populations representing distinct tritrophic niches have been surveyed.

## Implications of rapid environmental change for tritrophic niches

That anthropogenic environmental change affects biodiversity and ecological communities in non-random ways is fundamentally important to predicting its ecological consequences [22••]. Given that ecological niches are a community property, we argue that the biased effects of anthropogenic impacts have the potential to reconfigure tritrophic niches of herbivorous insects via bottom-up and top-down mechanisms. Non-random anthropogenic environmental impacts include heightened extinction risk of species at higher trophic levels [23,24], of large body size [25], with small geographic ranges [26], and with specialized habitats or hosts [27,28]. Conversely, some species benefit from such changes, and as ecological communities become increasingly composed of species that tolerate or benefit from anthropogenic environmental impacts [22••], we expect changes in both bottom-up and top-down dimensions of ecological niches of herbivorous insects. In an especially rigorous test of this issue, Harvey and MacDougall [29••] showed that habitat fragmentation, eutrophication, and defoliation homogenized insect herbivore and plant communities in experimentally manipulated grasslands. These homogenized communities consisted largely of geographically widespread plant species and polyphagous herbivore species [29••]. Because of the preponderance of host-plant specificity in herbivorous insects [30] as well as their great diversification in host-plant use, herbivore communities are likely to become increasingly simplified in taxonomic and functional diversity to the benefit of dietary generalist species [27,29••,31,32] and specialists associated with persistent plants in these transformed communities. Below, we review the anthropogenic environmental impacts of habitat fragmentation, climate change, and invasive species on insect herbivores and their implications for tritrophic niches.

## Habitat loss and fragmentation

Habitat fragmentation in the broad sense, consisting of reduced habitat patch size, increased isolation, and edge effects, is a pervasive impact of anthropogenic landscape transformation [33]. It renders unequal effects on species in ecological communities, thereby altering species composition and interactions [33,34,35,36]. Which species are most strongly affected by habitat fragmentation can determine its tritrophic outcome, such as increased or decreased predation, parasitism, or herbivory. In their meta-analysis of fragmentation's effects on resource consumption by terrestrial arthropods, Martinson and Fagan [35] found stronger reductions in resource consumption by predators compared to herbivores, consistent with the trophic rank hypothesis [23], as well as increased consumption by resource generalists and reduced consumption by specialists in fragmented landscapes. Together, these findings support the expectation that, within terrestrial food webs, specialized natural enemies of herbivores are most sensitive to the negative effects of habitat fragmentation [37,38]. Answering the call for studies that measure the effects of fragmentation on multiple trophic levels simultaneously, Genua *et al.*'s [39••] manipulative study of grassland patches found stronger fragmentation effects on predators than herbivores, resulting in trophic release of herbivores and increased herbivory [39••]. These effects of fragmentation were due to both direct effects (e.g. density) and trait-mediated indirect effects (e.g. altered behavior) depending on host-plant species examined [39••].

Negative effects of habitat fragmentation on herbivorous insects are strongly biased toward dietary specialists [40•], with effects on generalists being neutral [40•] or positive (e.g. [39••]). Although the specific causes of this pattern are not currently understood [38], habitat fragmentation may disrupt the interactions that create tritrophic niches of dietary specialist herbivores. As an illustration, Fenoglio *et al.* [41] found reduced parasitoid species richness and parasitism frequencies in a leaf miner community, resulting from the loss of host-specific parasitoids in small forest patches [41]. This example shows that bottom-up and top-down pathways of tritrophic systems are altered by habitat fragmentation (see [42] for a recent review).

## Anthropogenic climate change

Climate change can affect tritrophic interactions in several important ways. First, it can directly affect the physiology of herbivores and/or plants in ways that influence susceptibility to enemies [43–45]. For example, herbivore–microbe associations play important roles in mediating trophic interactions [46,47], and these associations are often highly sensitive to temperature [48,49]. Furthermore, defensive benefits of facultative symbionts of aphids against parasitoids can decline at higher temperatures [50]. The broad effects of climate change-altered interactions on herbivores are difficult to predict: poorer performance of an herbivore on its host plant could enhance (e.g. SGHM) or reduce (e.g. due to increased plant secondary metabolites) mortality from enemies; likewise for increased performance of herbivores. In either case, rapid coevolution is expected to attenuate effects of climate change on species interactions by dampening population fluctuations [51•].

Climate change may also directly affect enemies, altering the relative benefits of plant-based niches for herbivores. These effects are likely to be negative, particularly for parasitoids, as high trophic level and ecological specialization increases sensitivity to climate change [52]. Consistent with these predictions, climate change has been shown to increase herbivore biomass disproportionately over plants or parasitoids [53]. Such enemy-release should generally favor host-plant expansions in herbivores.

Finally, climate change can alter tritrophic interactions by changing the overlap in species in space or time due to differential range expansion or phenological responses [52,22••]. Such shifting distributions can allow colonization of novel hosts, alter competitive interactions, and modulate enemy pressures [52,54]. Colonization of novel host-plants in expanded ranges may provide EFS for herbivores, encouraging adaptation for increased feeding efficiency. Spatial or temporal escape from enemies may also relax selection for plant-associated defenses, further encouraging niche expansion. These predictions remain largely hypothetical as we are only beginning to empirically assess the ecological and evolutionary consequences of shifting ranges and phenologies [44]. One promising approach is laboratory simulation studies. In one such study, Carrasco *et al.* [55••] found negative effects of both an exotic herbivore and its parasitoid on a native herbivore-parasitoid system, even though the exotic parasitoid could not develop on the native host.

## Exotic species and novel communities

One of the most rapid anthropogenic environmental impacts is the establishment of novel species interactions through both introductions of alien species and distributional changes associated with climate change (above). Species introductions and invasions create novel ecological communities by ecological fitting [56], with limited mitigating effects of coevolutionary interaction. This process typically involves release from enemy pressure (e.g. [57•]) and thus profoundly shapes tritrophic niches. Simulation studies have suggested that exotic species can partially compensate for species loss due to climate change [58]. However, because exotic species lack a history of coevolutionary interactions in their new communities, they are at best unlikely to fill same roles as native species, and at worst can destabilize whole ecosystems.

Tritrophic niches of herbivores may be shaped by exotic species at each level: host plant, herbivore, enemy, or some combination of these. Introduced plants may initially be unrecognized by native herbivores or, if used, incur physiological costs [59]. However, novel host plants can provide EFS if enemies rely on host-plant associated cues to locate prey or if they provide novel defense against enemies [60]. Generalist herbivores should colonize exotic plants relatively rapidly, but more specialized feeders may also shift onto exotic host plants if they are phylogenetically or biochemically related to their original host(s) [61]. Over time, selection from both the bottom up and top-down can lead to genetic divergence of populations on native and novel hosts (e.g. [62,63]), and their natural enemies may follow [64]. Alternatively, enemies may constrain colonization of novel host plants if they do not provide the same degree of plant-mediated defense (e.g. crypsis, sequestered toxins) against enemies as native host plants (e.g. [65]).

Upon colonizing a novel environment, phytophagous insects can experience release from both enemies and coevolved plant defenses, sometimes with devastating ecological consequences (e.g. Emerald Ash borer, Hemlock wooly adelgid; [66]). Not only may these herbivores colonize plant taxa analogous to those used in their native range, but release from bottom-up and top-down constraints can lead to niche expansion onto more peripheral hosts (e.g. [67]). In addition to extreme herbivory or direct competition with natives, exotic herbivores may support increased densities of enemies, acting as a source of apparent competition [66,68]. Alternatively, multiple studies have shown that exotic herbivores can disrupt herbivore induced plant volatiles (HIPVs) that attract natural enemies to native herbivores [69,70]. Given sufficient time, selection by exotic herbivores may favor specific defense traits in plants and/or greater efficiency of enemies, but such re-establishment of coevolutionary processes has been little investigated.

The impact of introduced natural enemies on insect herbivore communities has mainly been studied in the context of biological control introductions and invasive social wasps and ants [66,71]. Invasive social Hymenoptera can dramatically affect entire ecosystems [72]. Exotic parasitoids should have milder impacts on herbivore

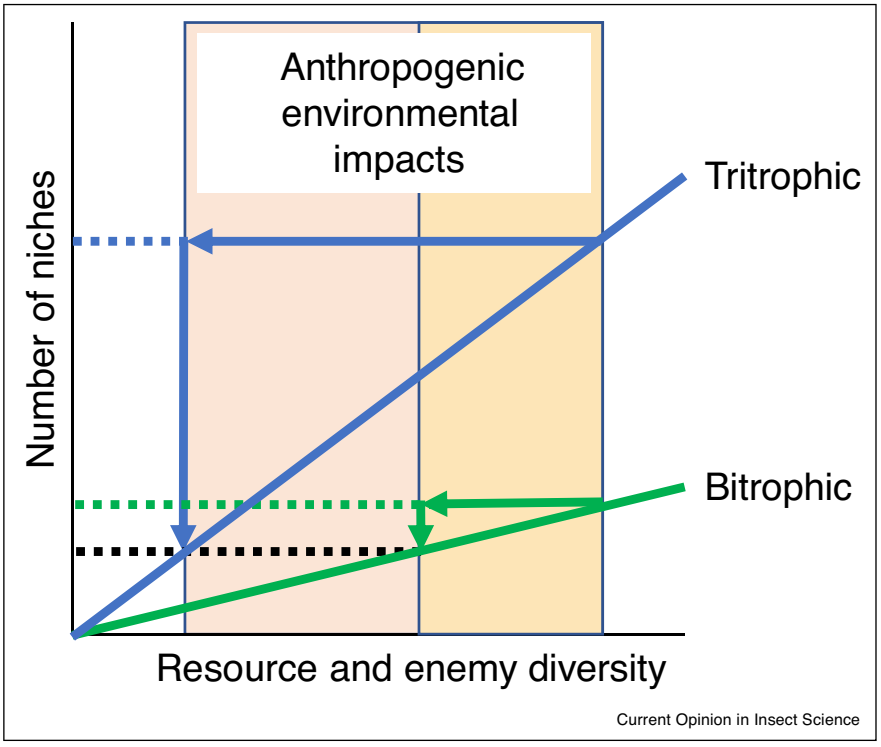
communities due to their greater specialization, although certain parasitoids may behave ecologically as generalist predators and cause broad community declines of native herbivores [71,73]. Interactions between invasive garlic mustard, native mustard white and exotic cabbage white butterflies (*Pieris* spp.), and their exotic parasitoids provide an insightful example of the complex ecological and evolutionary effects of exotic species in a tritrophic context [74•].

## Conclusions and areas for future research

Adopting a tritrophic niche perspective offers insight into potential responses of insect herbivores to rapidly changing environmental conditions. Aside from the bottom-up effects of herbivores tracking changes in their habitats and host plants, biased patterns of extinctions should progressively reduce the influence of large and ecologically specialized enemies, such as habitat-specific insectivorous birds [33] and host-specific parasitoids [41], and increase the influence of small and ecologically generalized enemies, such as invasive ants and wasps, effectively reducing tritrophic niche diversity. Consequently, we predict that the number of tri-trophic niches of herbivorous insects will become dramatically reduced (Figure 2). Because of the multiplicative effect of resource and enemy diversity on tritrophic niches, the loss of enemies as well as habitats and host plants (resources) is hypothesized to result in even sharper reductions in herbivore diversity (tritrophic niche diversity).

The ecological consequences of reduced tritrophic niche diversity are potentially severe. As herbivore niches become increasingly generalized and overlapping, more communities will resemble those in intensive agricultural landscapes. That is, insect herbivore population dynamics are likely to become more extreme and ecological effects of individual plasticity more powerful. The former prediction arises from the loss of specialized enemy diversity (Figure 2) and the concomitant release of herbivores from complementarity and stability in population control [75,76]. The latter prediction stems from the loss of tritrophic niches (Figure 2), which are predominantly occupied by ecologically specialized herbivores [30], yielding to a world of weedy generalists with high plasticity in feeding behavior [27]. Recent work shows that the magnitude of trait-mediated indirect interactions, such as trophic cascades, often hinges on behavioral plasticity of dietary generalist herbivores [77,78].

**Figure 2**




Hypothesized differences in herbivore niche loss due to anthropogenic environmental impacts when niches are assumed to be based on resources alone (bitrophic = green) versus resources and enemies (tritrophic = blue). As resource and enemy diversity is lost due to anthropogenic environmental impacts (horizontal arrows in boxed area), the number of niches is predicted to be reduced at different rates for bitrophic versus tritrophic niches (vertical arrows). Horizontal dashed lines facilitate comparison of the magnitude of bitrophic versus tritrophic herbivore niche loss. Note that human impacts are assumed to have a larger negative effect on specialized enemy diversity (left pink box) than on resource (i.e. plant) diversity (right beige box).

Yet, species' traits are not static, and insects, in particular, can evolve rapidly in response to changing environments. Persistent taxa are expected to evolve in response to selection associated with environmental change. Physiological tolerances will evolve, novel hosts will be colonized, novel enemies will be defended against. Such coevolutionary interactions are likely to mitigate the destabilizing effects of rapid environmental changes on communities, but the importance of such adaptation is difficult to predict. Even short term evolutionary responses are highly contingent upon both genetic and environmental constraints [79].

The tritrophic niche concept can serve future research as an organizing principle for unifying community ecology and evolution in the face of rapid environmental change. A major focus of future studies should be the integration of community ecology and evolution in this context with the ultimate goal of connecting genomic, physiological, and behavioral traits of species populations to community and ecosystem dynamics [77]. We advocate research programs that integrate a diversity of approaches, both experimental and observational. Observational studies of tritrophic community structure, diversity and distribution are essential for documenting the broad responses of communities to continuing environmental change, particularly if the data are gathered systematically such as to facilitate future comparisons. Environmental change offers 'natural,' often replicated experiments that can be exploited to understand adaptation in a tritrophic context (e.g. EFS associated with novel host-plants, tradeoffs in the evolution of defenses, coevolutionary interactions in fragmented landscapes). Long term, open access ecological data sets will be required to understand eco-evolutionary responses to changing environments. To the extent that long term community data sets are difficult to maintain and fund, we must also make more effective use of existing data and natural history collections, which can provide insight into changes in morphology (e.g. the famous peppered moth), distribution, phenology, ecological associations and to a growing extent, genetics. Novel tools (e.g. genomics, metabolomics, and environmental sensors) can also be harnessed to obtain novel forms and/or amounts of data that can complement more traditional ecological and evolutionary approaches. For example, high throughput sequencing of communities can provide rapid assessment of interactions (herbivore–host, predator–prey), including those that are 'non-permissive' [4••].

Connecting these observations to experiments with greater power to infer mechanisms is just as important. Common garden/greenhouse studies can be effective for analyzing how tritrophic relationships and selection vary with environmental conditions (e.g. [80]). The advent of powerful tools for measuring and manipulating genomes will enable common garden experiments to gain resolution in identifying genomic and epigenomic mechanisms of evolution and phenotypic plasticity. Multigenerational studies can allow fitness consequences of interactions and selection gradients to be more accurately estimated, providing predictive power in herbivore responses to environmental change. In addition, manipulative experiments set in natural ecological communities are critical for deducing causal relationships among the large array of variables at play in relatively unsimplified tritrophic systems. Tritrophic approaches have proven historically valuable in this context, and a key challenge will be integrating such experiments with longer term and larger scale studies so that our most powerful studies offer insights at the relevant scales of environmental impacts. In all of these efforts, it is key that researchers explicitly consider not only effects of enemies and resources, but the interactive effects of these forces, and that species are mutable; ecologically relevant traits shift and evolve, particularly when challenged with a changing environment.

## Conflict of interest statement

None declared.

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